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Aphanodactylidae, a new family of thoracotreme crabs (Crustacea: Brachyura) symbiotic with polychaete worms

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Abstract

The pea crabs of the family Pinnotheridae De Haan, 1833, have traditionally been recognised on the basis of their simplified external morphology, modified third maxillipeds, and general habit of living in association with invertebrate hosts, usually bivalve molluscs. Recent morphological and molecular studies of Pinnotheridae show that it is not a natural group as traditionally conceived. The subfamily Asthenognathinae Stimpson, 1858, actually belongs in the Varunidae H. Milne Edwards, 1853, and the subfamily Tritodynamiinae Števčić, 2005, is part of the Macrophthalmidae Dana, 1851. However, several 'pinnotherid' genera that are superficially similar to asthenognathines and allied to *Aphanodactylus* Tesch, 1918, appear to form a discrete group, but lack the chief synapomorphy of Pinnotheridae, namely, the highly modified maxilliped 3. Moreover, *Aphanodactylus* and allies do not share synapomorphies with of any presently recognised thoracotreme family. A new family, Aphanodactylidae, is therefore established for *Aphanodactylus, Gandoa* Kammerer, 2006, *Uruma* Naruse, Fujita & Ng, 2009, and a new genus and species described herein, *Gustavus mecognathus*. Aphanodactylids (where known) are symbiotic with terebellid polychaete worms and share short, stout, ambulatory legs with one or more spines lining the flexor margins of the ischiomeri of at least some of the ambulatory legs; a row of distal flexor spines on the ambulatory propodi opposing a claw-like dactylus; very short ambulatory dactyli that are less than half the respective propodus length; and marked sexual dimorphism in which the female is distinctly wider than the male. The phylogenetic position of Aphanodactylidae remains to be determined but the morphology of the third maxillipeds and the position of the male gonopore suggests that it may belong in the Pinnotheroidea, to which it is tentatively assigned. Each genus of the Aphanodactylidae is diagnosed and illustrated, and a key to the genera provided.

Keywords: Decapoda, Brachyura, Thoracotremata, Pinnotheroidea, Aphanodactylidae, Pinnotheridae, symbiosis, Polychaeta, Terebellidae

Introduction

The crabs of the family Pinnotheridae De Haan, 1833, have long been recognised as symbionts, usually living within the mantle chamber of bivalve molluscs or with polychaete worms. Most pinnotherids possess a relatively poorly calcified carapace with indistinct regions, have a highly modified maxilliped 3 and a simplified habitus, particularly with regards to the general lack of surface ornamentation. Among crabs traditionally regarded as pinnotherids were a group of genera that have long been placed in the subfamily Asthenognathinae Stimpson, 1858. Unlike most pinnotherids, which have a highly modified maxilliped 3, asthenognathines are atypical in having the ischium and merus as distinct segments, with the ischium larger than the merus, and the palp consisting of the carpus, propodus and dactylus clearly demarcated and not enlarged.

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Tesch (1918) recognized eight genera in Asthenognathinae: *Aphanodactylus* Tesch, 1918; *Asthenognathus* Stimpson, 1858; *Chasmocarcinops* Alcock, 1900; *Hapalonotus* Rathbun, 1897; *Mortensenella* Rathbun, 1909; *Opisthopus* Rathbun, 1893; *Tritodynamia* Ortmann, 1894; and *Voeltzkowia* Lenz, 1905. The classification of Asthenognathinae, however, has changed considerably since 1918 following more detailed studies of the morphology of these crabs. *Opisthopus* is a pinnotherine (see Schmitt *et al.* 1973); *Chasmocarcinops* a chasmocarcinid (see Schmitt *et al.* 1973; Ng *et al.* 2008); *Mortensenella* a camptandriid (see Harminto & Ng 1991); *Hapalonotus* a pilumnid (see Chia & Ng 1999); and *Tritodynamia* a macrophthalmid (subfamily Tritodynamiinae Števčić, 2005) (Števčić 2005; Ng *et al.* 2008). Most significantly, *Asthenognathus*, the type and only remaining genus in the subfamily Asthenognathinae Stimpson, 1858, is actually a varunid (see Cuesta *et al.* 2005; Ng *et al.* 2008). *Asthenognathus* shares numerous features with other varunids including the form of the thoracic sternum, male gonopore structure, male abdomen, gonopods and general structure of the pereopods (Ng *et al.* 2008). Although, taxonomic problems remain to be resolved within *Asthenognathus* and *Tritodynamia,* both being particularly speciose, Asthenognathinae *sensu stricto* nevertheless has varunid affinities; and as discussed, the other genera and species previously placed therein have been relatively easily reassigned to other families. That is, except for *Aphanodactylus*, *Gandoa* Kammerer, 2006 (replacement name for *Voeltzkowia*), the recently recognised *Uruma* Naruse, Fujita & Ng, 2009, and a new genus and species established below. Members of these genera (where known) are associated with terebellid polychaete worms and united by several distinct features: short, stout, ambulatory legs with one or more spines lining the flexor margins of the ischiomerus of at least some of the legs; a row of distal, flexor spines on the ambulatory propodus opposing a claw-like dactylus (to be confirmed in *Gandoa*); very short ambulatory dactylus that is less than half the respective propodus length; and marked sexual dimorphism in which the female is distinctly wider than the male (to be confirmed in *Gandoa* and *Uruma*). These genera form a discrete group but do not share synapomorphies of any presently recognised thoracotreme family. We therefore recognise a new family herein to accommodate these genera and species.

Materials and methods

Specimen measurements are given as carapace length (cl) and carapace width (cw), measured in millimetres (mm). The abbreviations P2–P5, G1 and G2 are used for pereopods 2–5, male first and second gonopods, respectively. Specimens are deposited in the Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii; Natural History Museum and Institute, Chiba (CBM), Japan; Muséum national d'Histoire naturelle (MNHN), Paris, France; The Naturalis (formerly Rijksmuseum van Naturrlijke Historie, RMNH), Leiden, The Netherlands; Ryukyu University Museum (RUMF), Fujukan, Okinawa, Japan; and Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, National University of Singapore.

Systematics

Pinnotheroidea De Haan, 1833

Aphanodactylidae n. fam.

Diagnosis. Carapace strongly sexually dimorphic (where both are known); female carapace transversely ovate to rectangular; male carapace narrower than that of female, ovate to subquadrate; surface glabrous or finely setose; smooth or punctate; regions poorly defined. Front deflected ventrally, faintly sinuous to bilobed in dorsal view. Orbital margins entire, well defined, infraorbital margin terminating mesially as angular tooth or rounded corner. Antennules folding transversely or obliquely. Antennae not excluded from orbit. Cornea pigmented. Maxilliped 3 ischium longer than merus, subquadrate or triangular; merus subquadrate; palp articulating at distolateral margin of merus, segments articulating end-to-end, decreasing in size distally; exopod with flagellum. Chelipeds equal; segments unarmed; surfaces smooth, finely to sparsely setose. Ambulatory legs relatively short, stout, P3 longest, P5 shortest, dorsal to other pereopods; P3–4 merus with row of spines or teeth on flexor margin; propodus distoflexor angle with 1 or more spines opposing dactylus. Dactyli short, claw-like, apices corneous. Female gonopore (vulva) on sternite 6, between suture 5/6 and 6/7. Male gonopore (genital papilla) emerging near anterior margin of sternite 8, distinctly mesial to coxa 8. Abdomen of female with all somites and telson distinct, mobile; males with somites and telson mobile or with somites 4–6 fused. Male abdomen narrowly triangular or linguiform.

Included genera. *Aphanodactylus* Tesch, 1918 [type genus], *Gandoa* Kammerer, 2006, *Gustavus* n. gen., and *Uruma* Naruse, Fujita & Ng, 2009.

Remarks. Members of the Aphanodactylidae n. fam. all have a rather uniform appearance: transversely rectangular or ovate carapace in females, narrower carapace in males; unornamented carapace surfaces with very little evidence of regionalisation; short, stout pereopods 2–4 with short, claw-like dactyli opposing spines on the distal propodal margins. These features of Aphanodactylidae are reminiscent of many Pinnotheridae *sensu lato* and are essentially the basis of earlier classifications placing aphanodactylids there. Some features remain to be confirmed for some genera; male *Gandoa* and female *Uruma* are, unfortunately, not yet known.

Aphanodactylids, however, differ significantly from all known Pinnotheridae in lacking the chief synapomorphy of pinnotherids, namely, the highly modified maxilliped 3. In pinnotherids the merus of maxilliped 3 is either considerably larger than, or fused with the ischium, forming a single unit (e.g., Ahyong & Ng 2007: fig. 1C); and the dactylus usually articulates proximally to the distal end of the propodus, and may be considerably enlarged or significantly reduced. Conversely, the maxilliped 3 of aphanodactylids is of the more typical, plesiomorphic thoracotreme form: the merus is smaller than the ischium and the palp is not enlarged. They resemble those found in a number of thoracotremes such as ocypodoids, and are what might be expected in stem-lineage Pinnotheroidea. Comparisons of the position of the male gonopores of aphanodactylids with specimens of other thoracotreme families revealed another noteworthy pattern. The position of the male gonopore in aphanodactylids, being distant from the base of coxa 8, closely resembles the condition of other pinnotherids (e.g., *Nepinnotheres*, *Arcotheres* and *Viridotheres*) as well as ocypodoids such as members of the Macrophthalmidae and Ocypodidae (see also Guinot 1979). As such, the overall pinnotherid-like habitus of aphanodactylids suggests that they are close to pinnotherids, though the plesiomorphic form of maxilliped 3 excludes them from placement within Pinnotheridae. Aphanodactylidae is therefore tentatively assigned to Pinnotheroidea, alongside Pinnotheridae. If our alignment of Aphanodactylidae with Pinnotheridae is correct, then the ocypodoid-like maxilliped 3 and male gonopore position might point towards some type of ocypodoid ancestry for Pinnotheroidea. Molecular investigations of the phylogenetic position of Aphanodactylidae and Pinnotheridae are currently underway by several investigators, although a close relationship between pinnotherids and ocypodoids has already been suggested by Wetzer *et al.* (2009) and to a lesser extent by Palacios-Theil *et al.* (2009).

All known members of the Aphanodactylidae, for which hosts are recorded, are associated with tube building polychaete worms (Terebellidae). The unusual distal propodal spines of the ambulatory legs, which oppose the dactyli forming a subcheliform structure, and teeth present on the flexor margins of some of the legs, possibly assists the crabs in holding onto the tube walls or the surface of their polychaete hosts. The four aphanodactylid genera can be distinguished by the key below.

Key to genera of the Aphanodactylidae

1. Maxilliped 3 merus triangular, inner distal angle produced to rounded lobe. Male abdomen with somites 4–6 fused . ... *Gustavus*
- Maxilliped 3 merus subquadrate, inner distal angle angular. Male abdomen with all somites free 2

2. P2–5 meri length about 1.5 times propodus and carpus length combined. P5 merus shorter than half length of P4 merus .... *Uruma*
- P2–5 meri as long as or slightly longer than propodus and carpus length combined. P5 merus exceeding half length of P4 merus 3
3. Carapace of females transversely subquadrate; surface distinctly punctate. .... *Gandoa*
- Carapace of females transversely ovate; surface smooth, with few scattered pits ....*Aphanodactylus*

Aphanodactylus Tesch, 1918

Aphanodactylus Tesch, 1918: 283 [type species: *A. sibogae* Tesch, 1918, by monotypy].

Diagnosis. Carapace wide, ovate, males 1.4–1.5 times wider than long, females 1.6–1.9 times wider than long; lateral margins cristate or subcristate, but not continuous to external orbital end; surface smooth, glabrous, with few scattered pits. Front narrow, deflexed broadly triangular in frontal view; straight to weakly sinuous in dorsal view. Orbit transverse; margins entire, unarmed; infraorbital margin mesially terminating in acute angle; supraorbital margin demarcated from antennular fossa by even curve; infraorbital and supraorbital margins not extending laterally beyond cornea or continuing laterally beyond orbit proper. Eyes short, mobile, fully occupying orbit. Antennules articulating transversely to slightly obliquely. Epistome short, medially sunken. Maxilliped 3 ischium longer than merus, both subquadrate. Thoracic sternites 1 and 2 completely fused, broadly angular anteriorly; sternites 2/3 demarcated by shallow groove; sternites 3/4 fused, laterally unarmed; sternites 4–8 demarcated by narrow grooves, those demarcating sternites 4–7 incomplete medially; without longitudinal groove. Cheliped merus and carpus unarmed, with sparse plumose setae. P2–5 similar in shape, P3 longest; meri about twice as long as high, as long as or slightly longer than respective carpi and propodi combined; with plumose setae on flexor and extensor margins; meri with or without teeth along flexor margin. P4 markedly shorter than preceding leg, dorsal to others. P2–5 with short spines on distoflexor angle of propodi opposing dactyli; dactyli very short, claw-like. Male abdomen simple, triangular; telson and all somites free; widest at somite 1; thoracic sternite 8 exposed when abdomen closed. Female abdomen with telson and all somites freely articulating, widest at somite 4. Vulva ovate, maximum width not exceeding half width of sternite 6. G1 simple, slender, broadly curved. G2 small, about 1/3 length of G1, slender, apex blunt.

Included species. *Aphanodactylus edmondsoni* Rathbun, 1932, *A. sibogae* Tesch, 1918, *A. loimiae* Konishi & Noda, 1999, *A. panglao* Ng & Naruse, 2009.

Material examined. *Aphanodactylus edmondsoni* Rathbun, 1932: BPBM 3576, holotype female (cl. 9.5 mm, cw. 16.1 mm), Oahu, Hawaiian Is., coll. C. H. Edmondson, 27 November 1931; BPBM 3577, 1 male (cl. 8.0 mm, cw. 11.6 mm), Oahu, Waimanalo, Hawaii, coll. C. H. Edmondson, 27 November 1931; ZRC 2000.0542, 1 male (cl. 8.2 mm, cw. 11.5 mm), 1 female (cl. 10.2 mm, cw. 16.9 mm), Oahu, Hawaiian Is., 1930s, coll. C. H. Edmondson. — *Aphanodactylus loimiae* Konishi & Noda, 1999: CBM 5341, 1 male (cl. 7.4 mm, cw. 10.3 mm), 1 ovigerous female (cl. 8.6 mm, cw. 13.9 mm), Kyan, Kuroshima I., Yaeyama Is., Ryukyus, 10 m deep, coral reef, in tube of *Loimia ingens* (Terebellidae), 10 October 1999, coll. K. Nomura on SCUBA; CBM 5443, 1 ovigerous female (cl. 9.1 mm, cw. 15.3 mm), Ahra Beach, Kume-jima I., Okinawa Is., Ryukyus, 10 m deep, coral reef, inhabiting tube of *Loimia ingens*, 15 June 1995, coll. K. Nomura on SCUBA. — *Aphanodactylus panglao* Ng & Naruse, 2009: NMCR, holotype ovigerous female (cl. 5.0 mm, cw. 8.8 mm) Napaling, Panglao I., Bohol Sea, Philippines, stn. B8, 3 m deep, 9°37.1′ N, 123°46.1′ E, by subtidal brushing of coral rock and debris, 7 June 2004, coll. Panglao Marine Biodiversity Project; ZRC, paratype male (cl. 3.1 mm, cw. 4.2 mm) (ZRC), Panglao I., Bohol Sea, Philippines, associated with an unidentified terebellid worm, early 2000s, coll. J. Hinterkircher. — *Aphanodactylus sibogae* Tesch, 1918: RMNH 2162, syntype female (cl. 5.4 mm, cw. 8.8 mm), east of Dangar Besar, Sapeh Bay, north coast of Sumbawa, Lesser Sunda Is., Indonesia, up to 36 m depth, SIBOGA Expedition st. 313, 14–16 February 1900; ZRC, 1 male (cl. 5.3 mm, cw. 7.8 mm), Sekotong, West Lombok, Indonesia, 16 May 2007, coll. D. L. Rahayu.

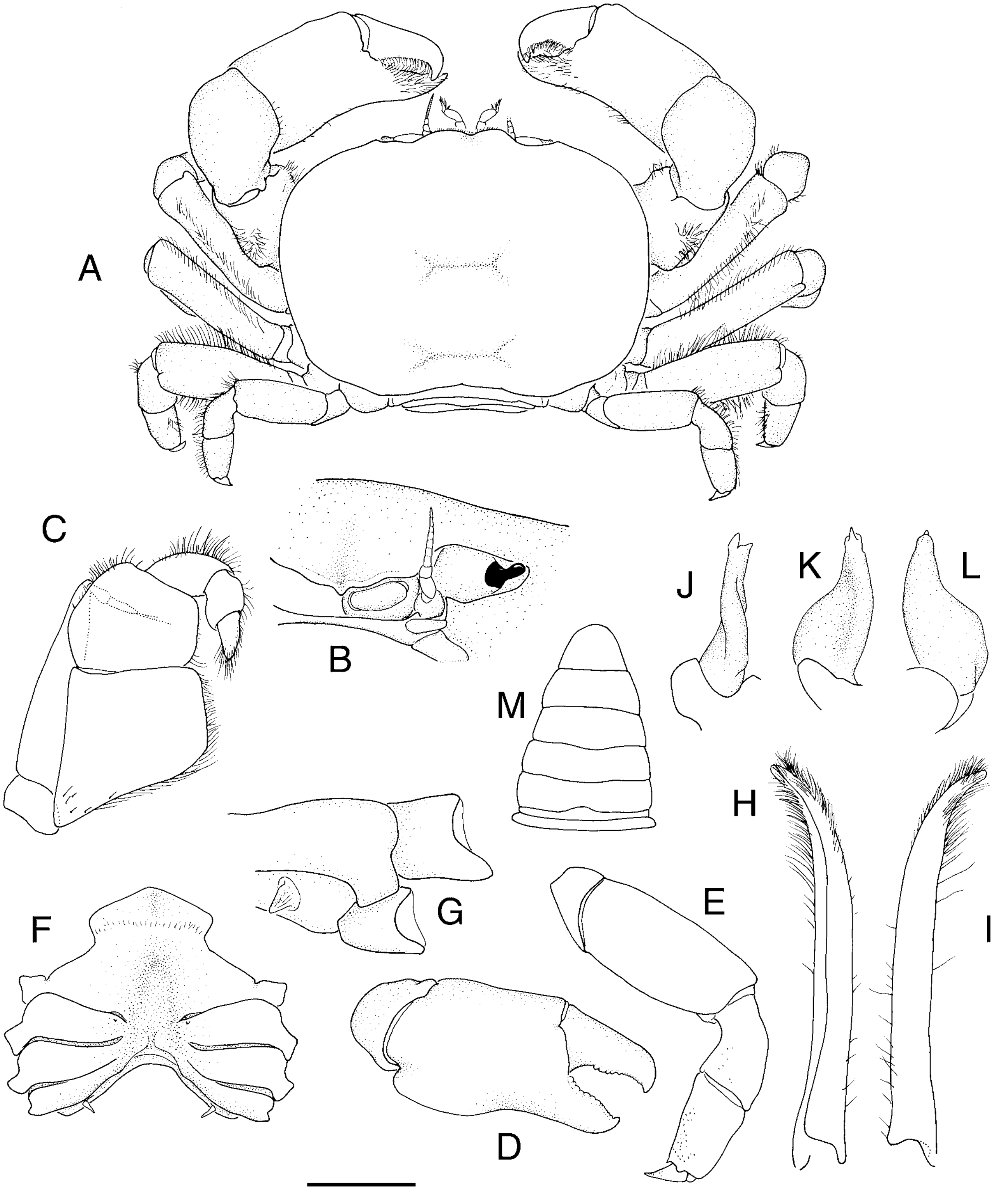

FIGURE 1. *Aphanodactylus loimiae*, male, cl. 7.4 mm, cw. 10.3 mm (CBM 5341). A, habitus. B, cephalothorax, anterior view. C, right maxilliped 3. D, right chela. E, right P5. F, thoracic sternum. G, left thoracic sternites 7–8, coxae, and genital papilla. H–I, left G1, abdominal and thoracic sternal views, respectively. J–L, left G2, mesial, sternal and abdominal views, respectively. M, abdomen. Scales: A, D, F, M = 3.0 mm; B, C, E, G = 1.5 mm; H, I = 1.0 mm; J–L = 0.5 mm.

Remarks. *Aphanodactylus* is the best known and largest genus of the aphanodactylids, and appears to be closest to *Gandoa* (see Remarks under the account of *Gandoa*). Four described species are presently known, all from the western Pacific and associated with terebellid polychaete worms. The taxonomy of these *Aphanodactylus* species has been treated and discussed in detail by Konishi & Noda (1999), Ng & Naruse (2009) and Ng *et al.* (in press). A male and female of *A. loimiae* are illustrated here to represent the genus (Figs. 1, 2).

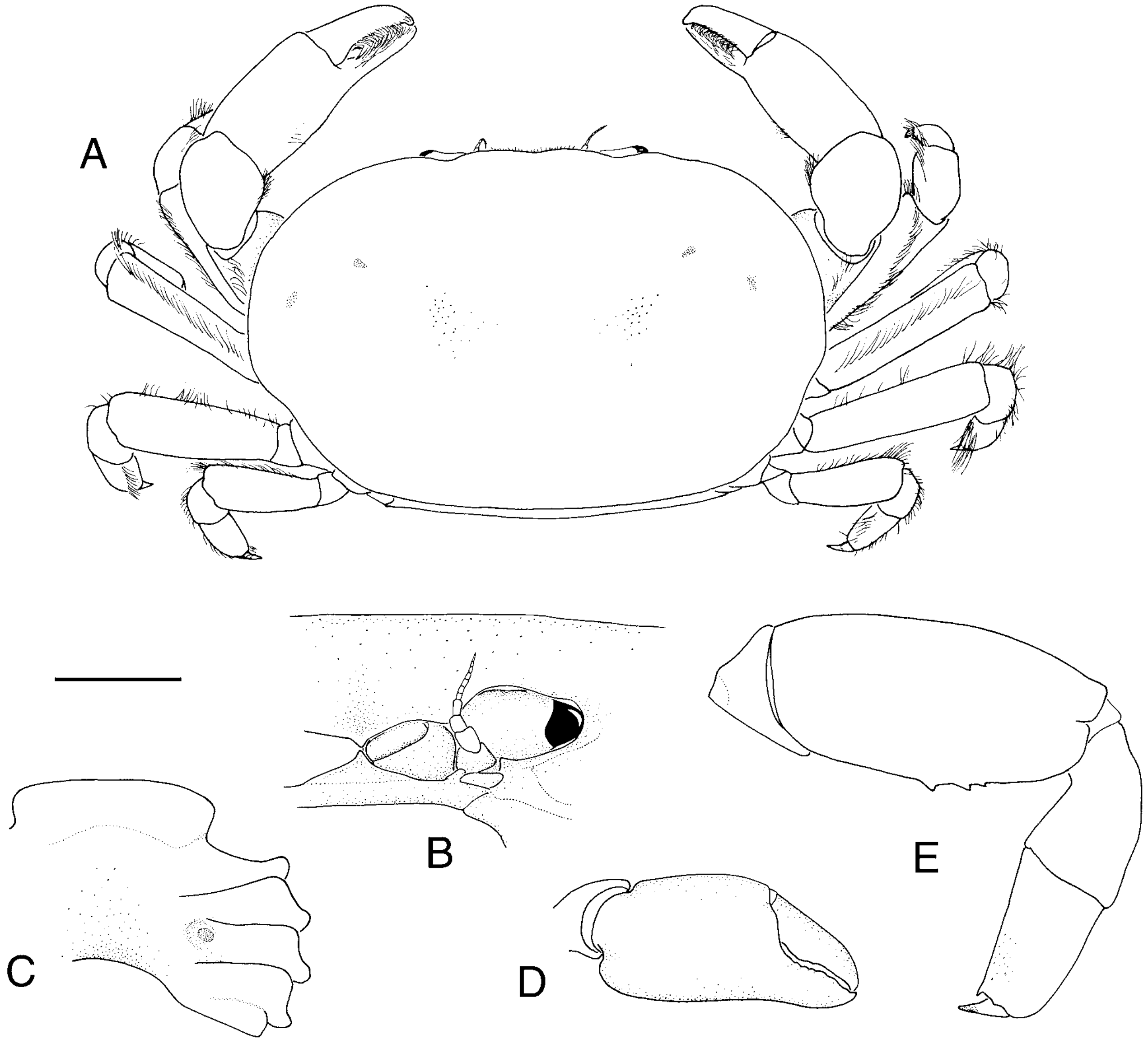

FIGURE 2. *Aphanodactylus loimiae*, ovigerous female, cl. 8.6 mm, cw. 13.9 mm (CBM 5341). A, habitus. B, cephalothorax, anterior view. C, thoracic sternum. D, right chela. E, right P4. Scales A, C, D = 3.0 mm; B, E = 1.5 mm.

Gandoa Kammerer, 2006

Voeltzkowia Lenz, 1905: 364 [type species: *V. zanzibarensis* Lenz, 1905, by monotypy].

Gandoa Kammerer, 2006: 270 [replacement name of *Voeltzkowia* Lenz, 1905, preoccupied by *Voeltzkowia* Boettger, 1893 (Reptilia)].

Diagnosis. Carapace wide, subrectangular, females 1.6 times wider than long; surface distinctly punctate. Front narrow, deflexed triangular in frontal view; broadly convex in dorsal view. Orbit transverse, normal;

orbital margins entire, unarmed; infraorbital margin mesially terminating in rounded angle; supraorbital margin demarcated from antennular fossa by even curve; infraorbital and supraorbital margins continuing laterally beyond orbit proper to form narrow, tapered slit. Eyes short, fully occupying orbit. Maxilliped 3 ischium longer than merus, merus subcircular; ischium subquadrate, widening distally, anterointernal angle acute. Cheliped merus and carpus unarmed, with sparse setae. P2–5 similar in shape, setose, P3 longest; meri about twice as long as high, about as long respective carpi and propodi combined; dactyli very short, claw-like. P4 markedly shorter than preceding leg, dorsal to others. Female abdomen with telson and all somites freely articulating, widest at somite 4.

Included species. *G. zanzibarensis* (Lenz, 1905) (Fig. 3), *G. brevipes* (H. Milne Edwards, 1853).

Material examined. *Gandoa brevipes* (H. Milne Edwards, 1853): MNHN B-10616, lectotype female (cl. 5.1 mm, cw. about 8.5 mm, carapace soft), Mayotte, Comoro Is., coll. Cloué.

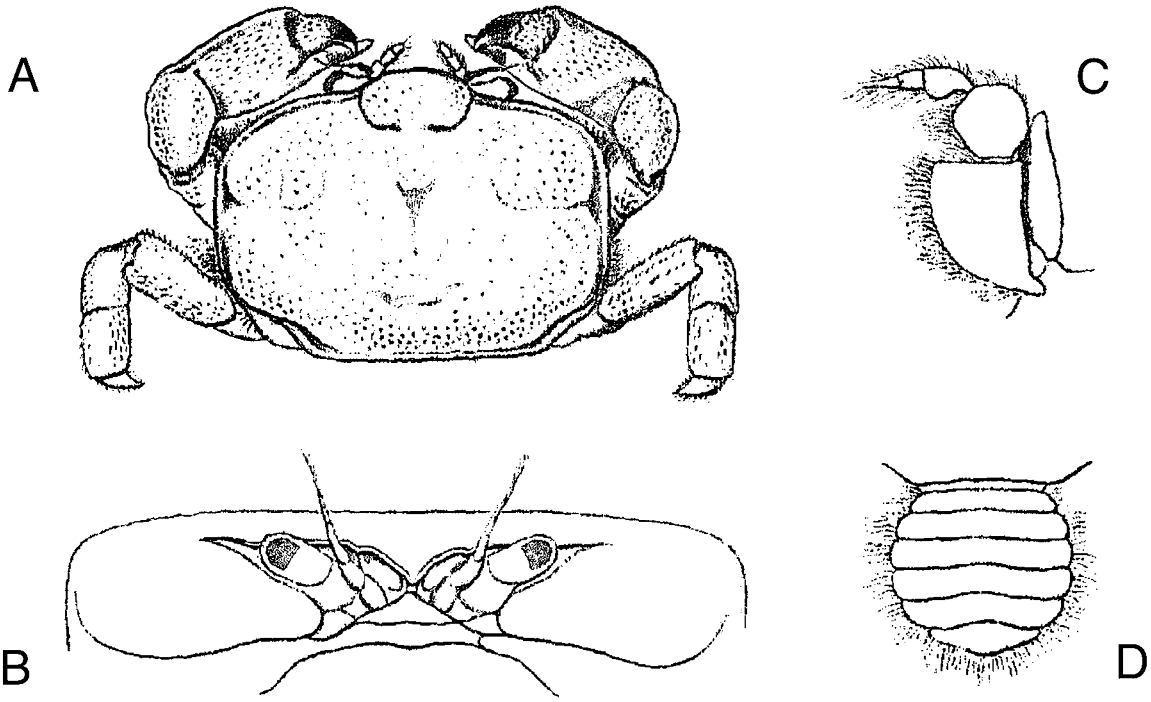

FIGURE 3. *Gandoa zanzibarensis* (Lenz, 1905), female holotype. A, habitus. B, cephalothorax, frontal view. C, left maxilliped 3. D, abdomen. (After Lenz 1905: pl. 47 figs. 9–9c).

Remarks. As has been discussed at length by Ng & Naruse (2009), *Pinnixia brevipes* H. Milne Edwards, 1853, from Mayotte, western Indian Ocean, is best placed in *Gandoa*. *Gandoa* is currently poorly understood, being known only from Lenz's (1905) account of the female holotype of *G. zanzibarensis*, and from the dried female holotype of *G. brevipes*. As can be deduced from comparison of the accounts of *Aphanodactylus* and *Gandoa*, very little actually distinguishes the two genera. The most important distinctions between *Aphanodactylus* and *Gandoa* appear to be the ovoid versus subrectangular carapace in females, the almost smooth versus distinctly punctate carapace surface, and the lateral continuation of the upper and lower orbital margins beyond the orbit proper in the latter. The upper and lower orbital margins in *Aphanodactylus* may or may not extend beyond the orbit proper, and thus appear to overlap with or approach the condition in *Gandoa*. The slight carapace shape differences between female *Gandoa* and *Aphanodactylus*, and differences in surface punctation are rather minor distinctions, raising the possibility that *Gandoa* might ultimately prove to be synonymous with *Aphanodactylus* (see Ng & Naruse 2009). These authors concluded, however, that until species of *Gandoa* can be more fully evaluated, and males are discovered and described, it is best to recognize *Gandoa* as a distinct genus. Moreover, the *Gandoa*-*Aphanodactylus* distinction correlates biogeographically, with both species of *Gandoa* occurring in the western Indian Ocean, and the four species of *Aphanodactylus* in the western Pacific. Thus, we follow Ng & Naruse (2009) in recognizing the two genera as separate pending further study.

Gustavus n. gen.

Type species. *Gustavus mecognathus* **n. sp.**, by present designation.

Diagnosis. Carapace wide, ovate to subpentagonal, males 1.4 times wider than long, females 1.8 times wider than long; lateral margins cristate but not continuous to external orbital end; surface finely pubescent, especially towards anterior half. Front narrow, deflexed medially, prominently triangular in frontal view; medially emarginate in dorsal view. Orbit transverse, normal; orbital margins entire, unarmed; infraorbital margin mesially terminating in rounded angle; supraorbital margin demarcated from antennular fossa by acute tooth; infraorbital and supraorbital margins not continuing laterally beyond orbit proper. Eyes short, mobile, fully occupying orbit. Antennules articulating obliquely. Epistome short, medially sunken. Maxilliped 3 covering buccal cavern; ischium slender, triangular, markedly longer than merus, inner distal angle produced mesially to form rounded lobe; merus rounded-subquadrate. Thoracic sternites 1 and 2 completely fused, broadly rounded anteriorly; sternites 2/3 demarcated by shallow groove; sternites 3/4 fused, laterally unarmed; sternites 4–8 demarcated by narrow grooves, those demarcating sternites 4–7 medially incomplete; without longitudinal groove. Cheliped merus and carpus unarmed, covered with short, fine, black-brown setae and some longer plumose setae on merus and carpus. P2–5 similar in shape, P3 longest; meri 3 or more times as long as high, slightly longer than carpus and propodus combined; covered with short, fine, black setae, especially on carpus and propodus, and longer plumose setae on merus to coxa. P5 markedly shorter than preceding leg, dorsal to others. P4 and 5 ischia and meri with prominent spines of flexor margins. P2–5 with short spines on distoflexor angle of propodi opposing dactyli; dactyli very short, claw-like. Male abdomen broad, linguiform, somites 4–6 fused; widest at somite 3; thoracic sternite 8 exposed when abdomen closed. Female abdomen with telson and all somites freely articulating, widest at somite 4. Vulva large, ovate, almost as wide as sternite 6. G1 simple, slender, strongly bent mesially at distal quarter. G2 small, about ¼ length of G1, slender, apex blunt.

Etymology. Named for Gustav Paulay, who collected the type material of *G. mecognathus*. Gender masculine.

Included species. Monotypic.

Gustavus mecognathus n. gen., n. sp.

(Figs. 4, 5, 7A)

Material examined. ZRC, male holotype (cl. 6.1 mm, cw. 8.8 mm), female paratype (cl. 8.0 mm, cw. 13.9 mm), SW Cocos Barrier, Guam, near small pass on large terebellid worm, G. Paulay, 20 March 2000.

Description. *Female:* Carapace ovate, distinctly broader than long, width to length ratio 1.8; dorsal surface smooth, regions poorly demarcated, scattered shallow pits; surface finely pubescent on surface and margins; lower lateral margins with dense plumose setae. Front deflexed, medially emarginate in dorsal view, triangular in anterior view, inner orbital margin rounded in dorsal view. Orbital margins entire, slightly narrowed laterally; eye filling orbit, cornea simple; infraorbital margin terminating mesially as rounded angle, supraorbital margin terminating mesially in slender, ventrally directed tooth. Anterolateral margin entire, convex laterally, cristate, continuing onto posterolateral margin but not supraorbital margin. Epistome very short, medially sunken. Antennule folding obliquely, filling fossa. Antennae with stout basal antennal article, not reaching distolateral angle of carapace; antenna not excluded from orbit.

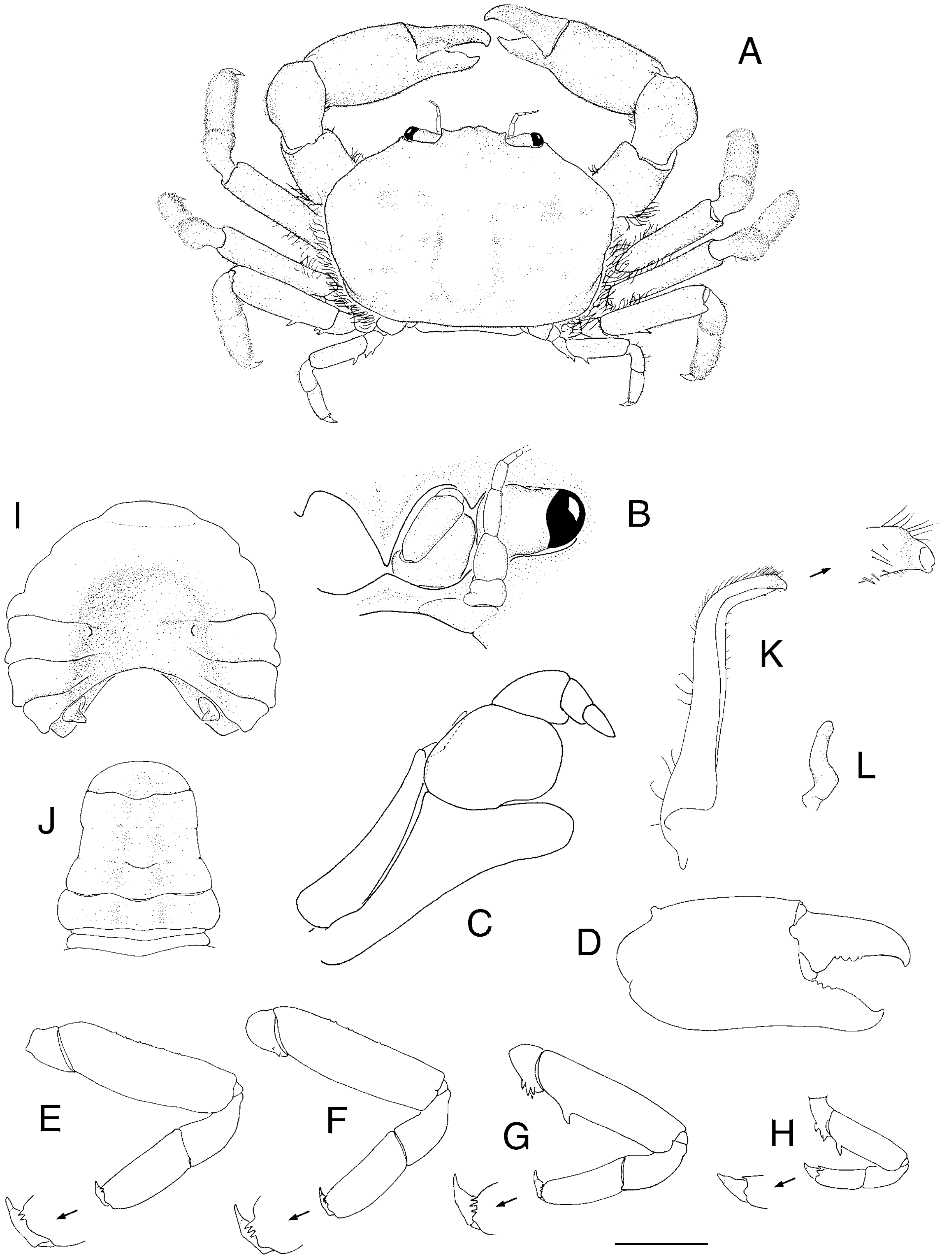

FIGURE 4. *Gustavus mecognathus* n. gen., **n. sp.**, male holotype, cl. 6.1 mm, cw. 8.8 mm (ZRC). A, habitus. B, cephalothorax, anterior view. C, right maxilliped 3. D, right chela. E–H, right P2–P5. I, thoracic sternum. J, abdomen. K, right G1, abdominal view. L, right G2, abdominal view. Scales: A = 2.9 mm; B, K–L = 1.0 mm; C = 0.7 mm; D–J = 2.0 mm.

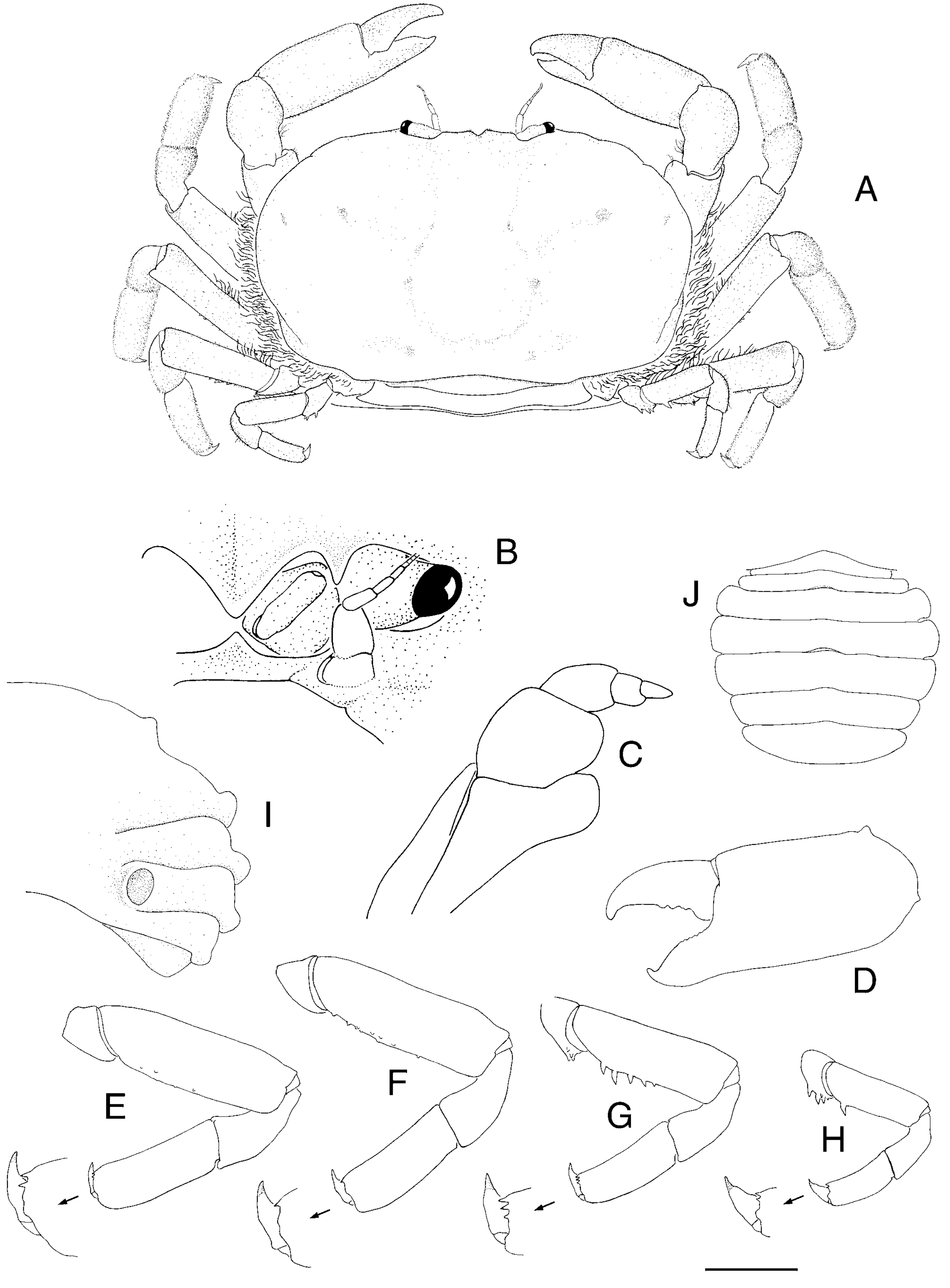

FIGURE 5. *Gustavus mecognathus* n. gen., **n. sp.**, female paratype, cl. 8.0 mm, cw. 13.9 mm (ZRC). A, habitus. B, cephalothorax, anterior view. C, right maxilliped 3. D, left chela. E–H, right P2–P5. I, thoracic sternum. J, abdomen. Scales: A = 2.9 mm; B, C = 1.0 mm; D–I = 2.0 mm; J = 4.0 mm.

Maxilliped 3 ischium distinctly longer than merus, slender, triangular, distomesial angle produced to rounded lobe extending mesially to level of mesial meral margin; merus smaller than ischium, slightly wider than long, rounded-quadrate: palp articulating on distal margin of merus; exopod slender, overreaching base of merus, flagellum short, not reaching distal margin of merus.

Chelipeds equal, covered with fine, short, black setae; merus triangular in cross section, with plumose setae proximally; carpus smooth, inner angle rounded with sparse plumose setae; chela surfaces smooth, palm about 1.4 times longer than dactylus; pollex with convex occlusal margin, crenulate proximally; dactylus occlusal margin with low, blunt teeth proximally.

P2–5 relatively short, P3 longest, P5 shortest, dorsal to other pereopods; propodus and carpus covered with short, fine, black-brown tomentum; merus with plumose setae along flexor and extensor margins; merus about 3 times as long as high, slightly longer than carpus and propodus combined; dactyli short, stout, apices corneous. P2 and 3 meri with scattered granules on flexor margin. P4 and 5 ischia and meri with stout spines on flexor margins. P2–5 propodi with 1–3 small distoflexor spines opposing dactyli.

Male: Carapace subpentagonal, broader than long, width to length ratio 1.4; dorsal surface smooth, regions poorly demarcated, scattered shallow pits; surface with fine, scattered setae on surface and margins; lower lateral margins with dense, plumose setae. Front deflexed, medially emarginate in dorsal view, triangular in anterior view, inner orbital margin angular in dorsal view. Orbital margins entire, slightly narrowed laterally; eye filling orbit, cornea simple; infraorbital margin terminating mesially as rounded angle, supraorbital margin terminating mesially in triangular, ventrally directed tooth. Anterolateral margin entire, convex laterally, cristate, continuing onto posterolateral margin but not supraorbital margin. Epistome very short, medially sunken. Antennule folding obliquely, filling fossa. Antennae with stout basal antennal article, not reaching distolateral angle of carapace; antenna not excluded from orbit.

Maxilliped 3 covering buccal cavern when closed; ischium distinctly longer than merus, slender, triangular, distomesial angle produced to rounded lobe extending mesially beyond level of mesial meral margin; merus smaller than ischium, slightly wider than long, rounded-quadrate: palp articulating on distal margin of merus; exopod slender, reaching almost to midlength of merus, flagellum short, not reaching distal margin of merus.

Chelipeds equal, covered with fine, short, black setae; merus triangular in cross section, with plumose setae proximally; carpus smooth, inner angle rounded with sparse plumose setae; chela surfaces smooth, palm about 1.2 times longer than dactylus; pollex with convex occlusal margin, with blunt teeth proximally; dactylus occlusal margin with low, blunt teeth proximally.

P2–5 relatively short, P3 longest, P5 shortest, dorsal to other pereopods; propodus and carpus covered with short, fine, black-brown tomentum; merus with plumose setae along flexor and extensor margins; merus about 3 times as long as high or greater, slightly longer than carpus and propodus combined; dactyli short, stout, apices corneous. P2 and 3 merus with scattered granules on extensor margin. P4 and 5 ischia and meri with stout spines on flexor margins. P2–5 propodi with 1–3 small distoflexor spines opposing dactyli.

Etymology. Derived from the Greek *mekos* for length, and *gnathos* for jaw, alluding to the elongate ischium of maxilliped 3.

Remarks. *Gustavus mecognathus* **n. gen.**, **n. sp.**, is perhaps the most peculiar of the aphanodactylids in the triangular rather than subquadrate maxilliped 3 ischium, broad male abdomen in which somites 3–5 are fused, and in the finely pubescent body surface, with longer, plumose setae around the bases of the pereopods and pterygostomian surfaces of the carapace. In all other aphanodactylids, the maxilliped 3 ischium is subquadrate, the male abdomen (not known in *Gandoa*) is narrowly triangular with all somites and telson freely mobile, and the carapace and most surfaces of the pereopods are glabrous. *Gustavus* differs from other aphanodactylids in numerous other features including: a sharply triangular instead of broadly angular front (in anterior view); strongly oblique articulation of the antennules (versus slightly oblique to near transverse); an acute process demarcating the supraorbital margin from the upper antennular fossa; and a rounded rather than angular mesial termination of the infraorbital margin.

Gustavus mecognathus has proportionally more slender ambulatory legs than other aphanodactylids. The ambulatory meri are about three or more times longer than high in *Gustavus* in comparison to about twice as long as high in *Aphanodactylus* and *Gandoa*. The P2–4 meri in *Uruma* are also about three times as long as high, though the legs are disproportionately larger in comparison to the carapace in *Uruma* than in *Gustavus.*

Distribution. Presently known only from the type locality, Guam.

Uruma Naruse, Fujita & Ng, 2009

(Figs. 6, 7B)

Uruma Naruse, Fujita & Ng, 2009: 60 [type species: *U. ourana* Naruse, Fujita & Ng, 2009, by monotypy].

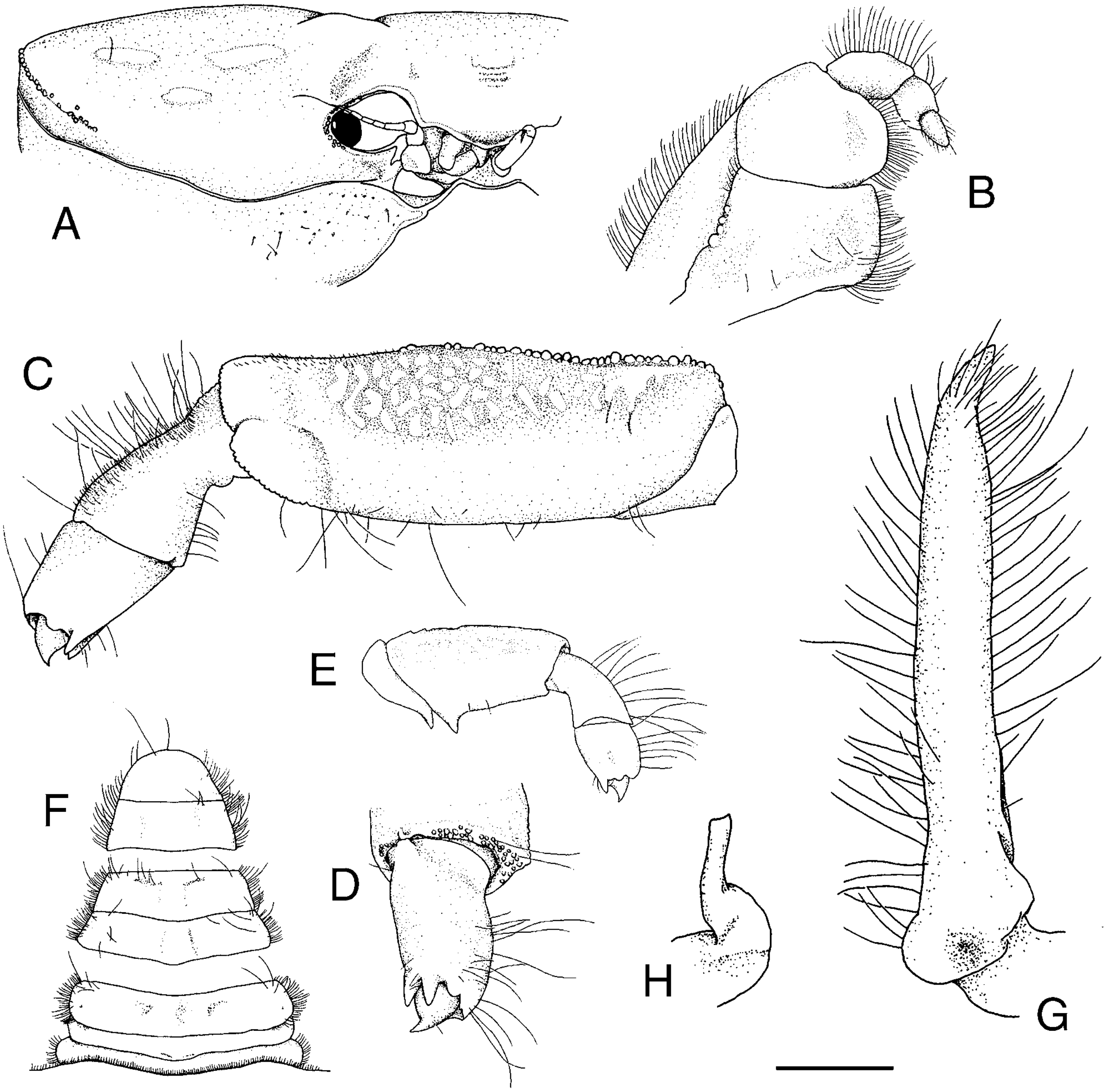

FIGURE 6. *Uruma ourana* Naruse, Fujita & Ng, 2009, male holotype, cl. 4.2 mm, cw. 9.2 mm (RUMF-ZC-907). A, cephalothorax, anterior view. B, right maxilliped 3. C, left P4, dorsal view. D, propodus and dactylus of left P4, ventral-inner view. E, right P5, dorsal view. F, abdomen. G, right G1, abdominal view. H, right G2, thoracic sternal view. Scales: A = 1.0 mm; B =0.8 mm; C, E = 1.5 mm, D = 1.3 mm; F = 2.0 mm; H, G = 0.5 mm. (After Naruse *et al.* 2009: figs. 3, 4).

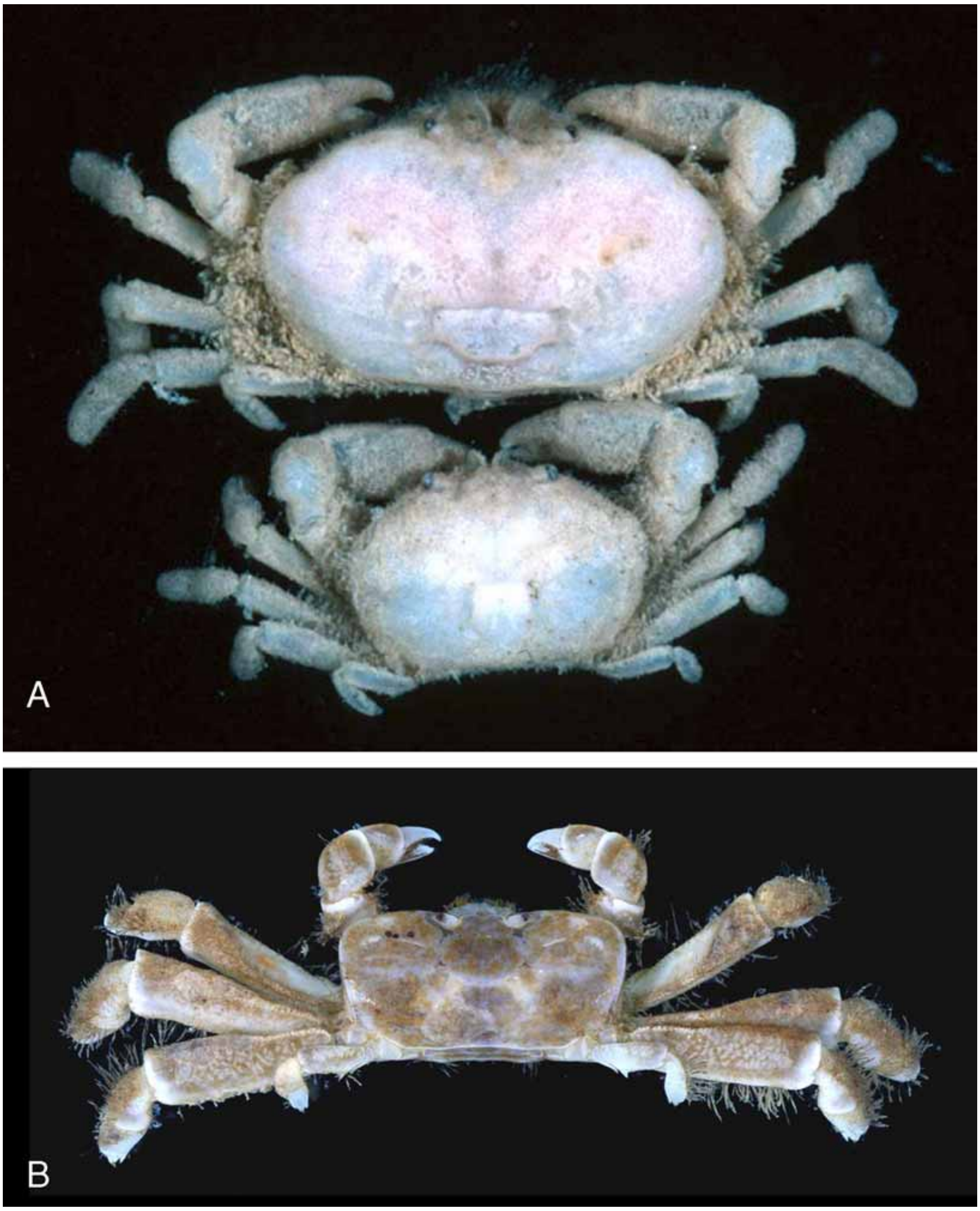

FIGURE 7. A, *Gustavus mecognathus* n. gen., **n. sp.**, male holotype, cl. 6.1 mm, cw. 8.8 mm (ZRC) (lower) and female paratype, cl. 8.0 mm, cw. 13.9 mm (ZRC) (upper) (photo: G. Paulay). B, *Uruma ourana* Naruse, Fujita & Ng, 2009, male holotype, cl. 4.2 mm, cw. 9.2 mm (RUMF-ZC-907) (after Naruse *et al.* 2009: fig. 1).

Diagnosis. Carapace wide, trapezoidal, margins cristate, but not continuous to external orbital end, epimeral suture just inferior to carapace proper; surface smooth, glabrous. Front narrow, deflexed medially, triangular in frontal view. Orbit oblique, mesial part of supraorbital margin placed more posteriorly than external orbital end; orbital margins entire, outer part granulated, infraorbital margin mesially terminating in sharp tooth; supraorbital margin demarcated from antennular fossa by obtuse angle; supraorbital margin demarcated from antennular fossa by acute tooth; infraorbital and supraorbital margins not continuing laterally beyond orbit proper. Eyes short, mobile, fully occupying orbit. Epistome short, medially sunken. Maxilliped 3 covering about 4/5 of buccal cavern. Thoracic sternites 1 and 2 completely fused, sternite 1 tooth-like, directed dorsally at proximal end of buccal cavern; sternites 2 and 3 demarcated by deep groove; sternites 3 and 4 fused, lateral parts marked by very shallow depressions and pits; sternites 4–8 demarcated by narrow lateral grooves at outside of sternal cavity, grooves ending at lateral parts of sternal cavity; sternal cavity depressed medially, no clear longitudinal groove. Cheliped merus with large transverse and triangular lobe on subdistal part of dorsal margin. P2–4 similar in shape, P3 longest; meri about 3 times as long as high, about 1.5 times length of propodus and carpus length combined; carpus longer than propodus. P5 merus slightly longer than carpus and propodus combined, about twice as long as high, just reaching proximal half of P4 merus; distal end of ischium and proximal end of merus each with single sharp tooth on flexor margin. P2–5 all with single pair of short, sharp claw on distoflexor angle of propodi; dactyli very short, claw-like. Male abdomen with all somites freely articulating, first somite widest. Thoracic sternite 8 exposed when abdomen closed, somite 3 to telson forming triangular outline. G1 straight, slender, distally tapering incurved. G2 small, about ¼ length of G1.

Included species. Monotypic.

Material examined. *Uruma ourana* Naruse, Fujita & Ng, 2009: RUMF-ZC-907, holotype male, cl. 4.2 mm, cw. 9.2 mm, Oura Bay, Okinawa , Ryukyu Is., Japan, 8 m, from a tube of unidentified worm, coll. M. Obuchi, 28 July 2007.

Remarks. *Uruma ourana* was recently described in detail by Naruse *et al.* (2009) and is presently known only from the male holotype collected from Okinawa.

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